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Topp, Emmeline N.; Tscharntke, Teja; Loos, Jacqueline

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Fire and landscape context shape plant and butterfly diversity in a South African shrubland

Emmeline N. Topp[1,2] | Teja Tscharntke[2] | Jacqueline Loos[1]

[1]Institute of Ecology, Faculty of Sustainability Science, Leuphana University Lüneburg, Lüneburg, Germany

[2]Agroecology, Department of Crop Sciences, University of Göttingen, Göttingen, Germany

Correspondence
Emmeline N. Topp, Faculty of Sustainability Science, Institute of Ecology, Leuphana University Lüneburg, Universitätsallee 1, 21335 Lüneburg, Germany.
Email: emmeline.topp@uni-goettingen.de

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Abstract

Aim: To understand effects of fire history and landscape composition on butterfly diversity in a fragmented agricultural landscape.

Location: We studied critically endangered renosterveld remnants within the fynbos biome in the Swartland municipality, Western Cape, South Africa, a global biodiversity hotspot.

Method: We selected survey sites on renosterveld fragments in the agricultural landscape along a gradient of fire history to test the response of biodiversity patterns to fire and landscape composition. We surveyed butterfly species richness, abundance and community composition as well as vegetation structure in five survey rounds on 58 sites between August 2018 and April 2019. We analysed data through linear modelling and multidimensional scaling.

Results: Fire was associated with reduced shrub and understorey plant cover and with increased plant species richness. Butterfly species richness was three to four times higher when natural habitat increased in the surrounding landscape (within a 2 km radius), while butterfly abundance was negatively associated with increasing time since fire, with approximately 50% fewer individuals after 9 years. Fire was indirectly associated with increased butterfly species richness and abundance through the alteration of vegetation structure, particularly through removal of shrubs and enhanced plant diversity. Low-mobility butterfly species were more positively associated with less vegetation cover than were high-mobility species, which were more associated with sites characterized by long absence of fire.

Main conclusions: Our findings suggest that species respond differently to fire, so a diversity of fire frequencies is recommended. Partially burning areas approximately every 10 years may benefit particularly low-mobility butterfly species through gap creation and fostering plant diversity. Hence, including fire into management activities can benefit butterfly and plant populations alike in critically endangered renosterveld.

KEYWORDS

cape floristic region, fire management, fragmentation, fynbos, natural disturbance

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1 | INTRODUCTION

For effective management and conservation of natural habitat, it is essential to consider natural disturbance regimes. Fire is a key natural disturbance, which alters vegetation and affects animal movement in landscapes (Nimmo et al., 2019). In fragmented fire-prone landscapes, the spatial context and composition of remaining habitat fragments shape the outcomes of the fire regime (Parr & Andersen, 2006). Remaining natural habitat fragments within agricultural landscapes are important refuges for insect diversity, including butterfly diversity. In biodiversity hotspots, these natural remnants are particularly important for maintaining biodiversity and are thus conservation priorities in the face of global insect decline (Brooks et al., 2006; Fonseca, 2009; Hallmann et al., 2017). While habitat loss is widely accepted as a principal driver for declining insect populations, quality of habitat is a further key factor determining species survival (Henderson et al., 2018). In fire-prone biodiversity hotspots, which experience strong colonization–extinction dynamics (Cleary & Mooers, 2006; Fernández-Chacón et al., 2014; Schurr et al., 2007), the role of remaining habitat in the landscapes may be more important for insect conservation than in landscapes characterized by more stability.

Landscape context, fire and habitat quality are all drivers of butterfly diversity. While traditional species–area relationships have been observed for butterflies in many fragmented landscapes (e.g. Bruckmann et al., 2010), multiple small habitat fragments can support butterfly populations in agricultural mosaics (Fahrig, 2020; Rösch et al., 2015; Tscharntke et al., 2002). Landscape context attributes, such as the amount of natural habitat in the focal landscape, are increasingly recognized as a driver of arthropod diversity (Aviron et al., 2005; Hendrickx et al., 2007), particularly for mobile taxa such as butterflies (Krauss et al., 2003). Butterfly populations also respond to fire in grasslands and shrublands (Henderson et al., 2018; Moranz et al., 2014; Vogel et al., 2007). The effect of fire may be direct, through loss of individuals, or indirect, as fire regimes can alter host plant availability and vegetation structure, which provide important resources for butterflies (Pywell et al., 2004; Vogel et al., 2007). In addition, butterflies with differing traits may respond differently to drivers at different spatial scales (Loos et al., 2015). For example, low-mobility butterflies and habitat specialists may require specific habitat retention in intensively managed landscapes (Toivonen et al., 2016) and may require targeted fire regimes to enhance population survival (Schultz et al., 2018). However, highly mobile butterflies may be able to move far distances through a fire-prone landscape to make use of available resources (Baum & Sharber, 2012).

The renosterveld ecosystem of the Cape Floristic Region (CFR), a global biodiversity hotspot, is a fire-prone shrub-scrub ecosystem belonging to the fynbos biome, which is now one of the most critically endangered habitats in South Africa (Bergh et al., 2014). Approximately 95% of West Coast renosterveld in the Western Cape has been lost to agricultural transformation and urbanization, much of which occurred throughout the 20th century (von Hase et al., 2003; Newton & Knight, 2005). Renosterveld is considered a fire-driven ecosystem which becomes more shrub-dominated in the absence of fire, although it contains fewer fire-adapted plant species than fynbos (Heelemann, 2010; Kraaij & van Wilgen, 2014). In pre-colonial times, native herbivores would also have driven renosterveld diversity patterns, given the abundance of palatable grasses. Several studies have shown the combined effects of fire and grazing on renosterveld vegetation dynamics. For example, many renosterveld annual and geophyte species are vulnerable to grazing once they regenerate following fire (Curtis, 2013; Helme & Rebelo, 2005; Kraaij & van Wilgen, 2014) and grazing following fire can enhance the dominance of shrub (Radloff et al., 2014). Remaining renosterveld patches are mostly privately owned and often not managed for their biological value, but either left unmanaged by land managers or used for grazing of domestic cattle and sheep (Winter et al., 2007). While being known primarily for its exceptional plant richness, particularly geophytes, renosterveld also fosters high insect diversity (Stander, 2016; Vrdoljak & Samways, 2014), including endemic and rare species. For optimal plant regeneration and removal of dominant shrub, it is recommended that renosterveld patches are burned approximately every 10–15 years (Esler et al., 2014; Kraaij & van Wilgen, 2014). Limited understanding of insect ecology in renosterveld (Topp & Loos, 2019a) makes it difficult to assess how fire regimes may impact insect diversity in the fynbos biome (Procheş & Cowling, 2006), although it has been shown that bees may benefit from flower abundance resulting from regular burns in the CFR (Adedoja et al., 2019) and ecologically appropriate fire management is key to support diverse butterfly populations elsewhere in South Africa (Gaigher et al., 2019). Given the importance of understanding management impacts and ecological processes in renosterveld (Topp & Loos, 2019a) and the inclusion of habitat and landscape conservation as key strategies for butterfly conservation in South Africa (Edge & Mecenero, 2015), our intention was therefore to investigate the relationship between fire in renosterveld and butterfly diversity in the CFR.

Renosterveld fragments are known to foster diverse butterfly populations (Topp & Loos, 2019b), even though their species richness is lower than in lowveld savannah or forest biomes of South Africa (Dobson, 2018). On average, a total of 7–11 butterfly species per day are expected to be observed in the fynbos-renosterveld biome (Dobson, 2018). West Coast renosterveld fragments have previously supported endangered species including the Moorreesburg Common Opal (*Chysoritis thysbe schlozae*) and Dickson's Brown (*Stygionympha dicksonii*), although none have been recorded since 2009 (Southern African Lepidoptera Conservation Assessment, 2017). These highly localized and rare species, as well as many other species occurring on renosterveld, are polyphagous species (Woodhall, 2005). Many species' larval host plants can be found in similar South African biomes such as fynbos and succulent karoo (SALCA, 2017). While no butterfly species are known to feed on plants exclusively found in renosterveld, some species can be relatively uncommon or found in a

limited geographical region which includes renosterveld, including the aforementioned endangered species, and non-threatened species such as the Tulbagh Sylph (*Tsitana tulbagha tulbagha*) (SALCA, 2017). Other renosterveld-occurring butterfly species of the Lycaenidae family are myrmecoxenous, meaning the larvae rely on or benefit from feeding and shelter in ant colonies. Such species include the Boland Skolly (*Thestor protumnus)*, the Pan Opal (*Chrysoritis pan)*, the Dull Copper (*Aloeides pierus*) and the Pointed Copper (*Aloeides apicalis*). Colonies of these butterfly species may only occur in restricted ranges of up to 100m in diameter (SALCA, 2017). Suitable ant species colonies for associative or obligatory relationships with these butterflies may be found in areas of natural habitat. Thus, renosterveld remnants may provide some of the only suitable conditions for some species with specific habitat requirements in otherwise transformed landscapes of the CFR, where much natural habitat is lost. Bowie and Donaldson (1999) emphasized the importance of connectivity of remnants for the Cupreous Blue (*Eicochrysops messapus*), which occurs in the CFR and more widely through South Africa (Woodhall, 2005). Both local and landscape scale attributes of renosterveld can therefore play a role for renosterveld butterflies (Topp & Loos, 2019b), although to date we are not aware of studies that have focused specifically on the response of butterflies to fire in renosterveld at a landscape scale.

Our overarching research question is: How does butterfly diversity vary along a disturbance gradient of time since last fire and landscape context in remaining renosterveld fragments? In addressing this question, we also aim to derive management recommendations for effective conservation of butterfly diversity in fragmented and fire-prone renosterveld. We first investigate the relationship between time since the last fire and vegetation diversity and structure in order to assess the link between fire history and potential plant and floral resources. We then investigate the relationships among vegetation diversity and structure, time since last fire and landscape context with butterfly diversity, in terms of butterfly species richness, abundance and composition. Previous studies in other grassland ecosystems have shown that recently burned sites had similar or higher butterfly abundances to fire-excluded sites (e.g. Henderson et al., 2018; Panzer & Schwarz, 2000) which is in contrast to the hypothesis that butterfly abundance would be higher in fire-excluded sites (Panzer & Schwarz, 2000). We hypothesized that recently burned renosterveld sites would have higher plant diversity and, correspondingly, higher butterfly species richness and abundance than unburned sites. We also hypothesized disturbance through fire to be more strongly negatively associated with low-mobility species than high-mobility species, which should be able to move more freely through the landscape and make use of patches of varying burn ages. Nearby natural habitat is an important factor for butterflies and in a fire-prone landscape could potentially enable butterflies to recolonize recently burned areas. We therefore hypothesized that more natural habitat in the surrounding landscape would also benefit butterfly diversity in focal fragments.

2 | MATERIALS AND METHODS

2.1 | Study region

Our study area was the Swartland municipality and its close surrounding, Western Cape, South Africa, approximately 60km north of Cape Town (Figure 1). The region has a Mediterranean-type climate with winter rainfall and hot, dry summers. The land use is predominantly grain farming, including wheat, oats and barley, along with livestock, wine grape and vegetable production. The majority of the remaining renosterveld is West Coast renosterveld, which grows on relatively fertile soils that are also nearly always clay-rich (Henning et al., 2009). Renosterveld is comprised of small-leaved, evergreen shrubs with an understory of grasses and high proportion of geophytes (Bergh et al., 2014). Remaining renosterveld fragments are mostly privately owned and occur on steep hillsides, which cannot easily be cultivated. Fragments vary greatly in size, with the majority of larger fragments on the borders of the Swartland municipality, although several large (>1,000 ha) fragments remain within the agricultural landscape. It is common for Swartland grain farmers to annually burn the wheat stubble fields during autumn (March–April). These burns are normally closely controlled, and any adjacent renosterveld is seldom burned. Fires in remaining renosterveld may be either accidental due to human negligence (e.g. sparks from farming machinery) or, more rarely, in fragments which are managed as reserves, deliberately initiated by the land manager to remove shrubs and regenerate floral diversity. Renosterveld fragments which have not been subject to fire in the previous ten to fifteen (approximate) years are often dominated by mature bushes such as renosterbos (*Elytropappus rhinocerotis*), kraalbos (*Galenia africana*) or kapokbos (*Eriocephalus africanus*). Some renosterveld fragments are grazed in either high or low intensity, mostly by sheep and cattle, although renosterveld is rather seen as supplementary grazing provision for when croplands are growing and cannot be used for grazing (Curtis, 2013).

2.2 | Site selection

We selected 50 renosterveld fragments across the Swartland as study sites to cover a gradient of time since the previous fire and a range of different fragment sizes (between 0.7 ha and 4,227.6 ha, median 22.6 ha). Thirty-two of our study fragments were selected from a previous study on butterflies in renosterveld (Topp & Loos, 2019b). Eight of our study fragments were designated nature reserves under either private or public ownership, and 42 were privately owned. Eight study fragments contained patches of different fire ages (Figure 2a–c), so we considered these as separate sites and sampled them separately, resulting in 58 sampled renosterveld sites overall. We identified the time since previous fire for each site by checking two GIS datasets: all fires on Cape Nature properties from 2016 to 2017 (Western Cape Nature Conservation Board, 2017) and the Moderate Resolution

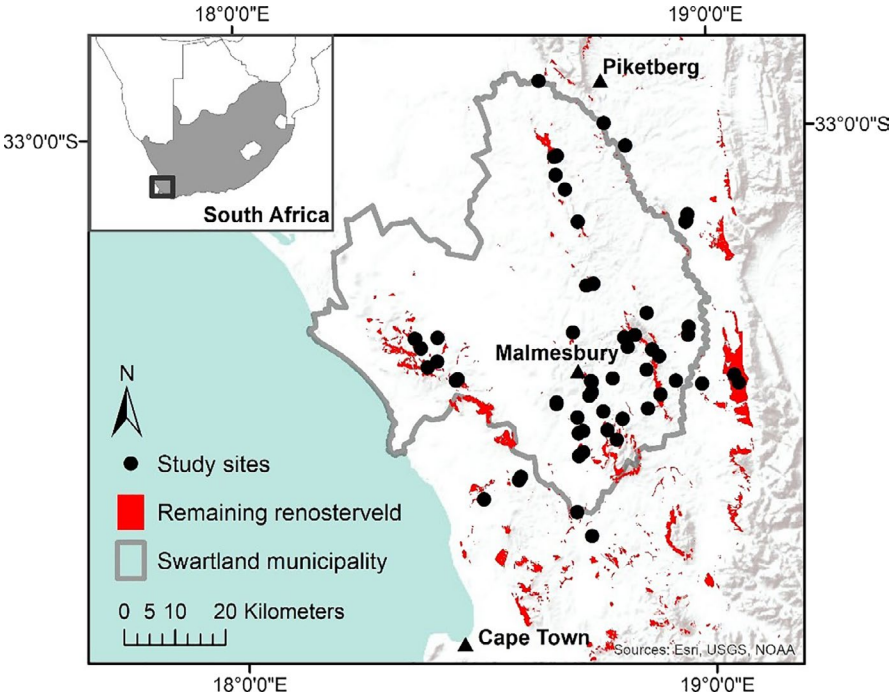

FIGURE 1 Map of the study region. The 58 study sites lie within the Swartland municipality and its close surrounding and are shown as black circles. Notable towns and cities are shown as black triangles

Imaging Spectroradiometer (MODIS) data for the Swartland municipality from 2002 to 2018 (MODIS Collection 6, 2018). We also checked sites visually using freely available historical satellite imagery (Google Earth Pro Version 7.1.8.3036). We confirmed time since last fire and grazing regime with local experts and the land owner or manager. Study sites of known burn age ranged from 1 to 16 years since last fire and may have burned accidentally or through prescribed burning.

For sites of more than 16 years since the last fire, we could not be certain of the exact year due to lack of accurate remote-sensing data and approximate information by landowners, and therefore, we categorized these sites separately as 16+ years. We did not include these sites in the subset of data for linear modelling of fire on vegetation and on site-level butterfly diversity (*n* sites = 21). We categorized grazing regime into three types: heavily grazed, lightly grazed and non-grazed. We obtained information on fragment sizes from the South African National Biodiversity Institute (SANBI) spatial data layer of mapped remaining renosterveld fragments, accessed through the SANBI GIS repository (http://bgis.sanbi.org). To investigate the landscape context, we calculated the amount of natural habitat (renosterveld and non-renosterveld vegetation) within a 2km radius of the survey location in each site. In lieu of detailed information on butterfly dispersal in our study area, we selected this distance as it is known to allow for dispersal of butterflies in other fire-prone landscapes (Henderson et al., 2018). However, we acknowledge that butterfly dispersal can be highly variable. Furthermore, we investigated the landscape context through the number of neighbouring fragments within a 5 km radius, in GIS using the same renosterveld fragment data layer. We measured a 2 km radius from the centroid of butterfly sampling GPS points, and thus, the amount of natural habitat in the surrounding 2 km included the selected fragment itself (Rand & Tscharntke, 2007; Spiesman et al., 2017). Therefore, larger selected fragments by definition had larger amounts of natural habitat in the surrounding, but smaller selected fragments may also have large amounts of natural habitat in the surrounding if they were located within 2 km of other natural habitat fragments. The amount of natural habitat in the surrounding 2 km from the surveyed locations ranged between 1.41 ha and 1,224.9 ha (median 91.34 ha).

2.3 | Butterfly and vegetation recording

We visited each of the 58 renosterveld sites five times in total; four times during the spring–summer period of August–December 2018 and once in the autumn period of March–April 2019, to maximize the opportunity to detect species of different flight periods and voltinism. We conducted surveys on days with a temperature of at least 17°C and extended dry periods between 9.30 a.m. and 5 p.m. (Pollard, 1977; Terblanche & Edge, 2011). During each round, we changed the time of day that we surveyed each site to capture temporal variation in butterfly activity. Two fieldworkers each walked four separate random transects through the renosterveld of 5 min in duration, so that each site was surveyed a total of 40 min per survey round. Fieldworkers walked at least 20m apart to cover different areas of the site, while remaining within eyesight of each other. Each fieldworker walked at a steady pace, slow enough to spot butterflies which may be moving low to the ground, surveying the area approximately 4m either side of the transect, similar to Leone et al., (2019) and recommended by Terblanche and Edge (2011). During each transect walk, we counted and recorded all butterflies seen and aimed not to record the same individual twice. Where possible, we recorded butterflies to species level in flight. Where the butterfly species was uncertain, we captured, photographed and released the individual, which was later identified by a local expert (see Acknowledgements).

FIGURE 2 (a) Koringberg (−33.045718, 18.673489), one of the larger renosterveld study fragments in the Swartland region, with both recently burned (3 years prior to study, light green young growth, left hand side of photograph) and unburned (more than 30 years since last fire, dark green woody vegetation, in foreground and on right hand side of photograph) patches. (b) The lower east-facing slope of Contreberg (−33.450922, 18.465570) which has not burned in more than 20 years, and (c) the upper part of the slope, which burned accidentally in 2017. Photographs: E. Topp 2018

At the end of each 5-min transect, each fieldworker sampled a representative 2 × 2 m vegetation plot, in which the species richness of plants and vegetation structure-related variables were recorded (Table 1). As we walked random transects during each visit, we sampled the vegetation on every visit, resulting in a total of 2,320 transects (40 plots/site).

2.4 | Data analyses

We analysed the data in five steps. We first investigated how fire is related to vegetation at the transect level, where each transect was an individual observation in the dataset. To this end, we calculated generalized linear mixed models for each vegetation variable (Table 1) as a response variable, using time since fire as an explanatory variable. We used the subset of the data with time since last fire as a continuous variable (*n* sites = 21), treating fragment and survey round as random factors. In this subset, two sites were heavily grazed, two were lightly grazed and 17 were not grazed; thus, we did not have an optimal number of observations per grazing category to include grazing as a random effect. We therefore included grazing as an explanatory variable to account for possible correlations, although we did not design the study to test this variable. As we had few sites with very large amounts of natural vegetation and many sites with small amounts of natural vegetation in the surrounding, we square-root transformed the amount of natural habitat to account for this imbalance (e.g. Steffan-Dewenter & Tscharntke, 1997). This step also takes into consideration the species–area relation, which saturates following a steep incline. For shrub height, we first used a binomial model to see whether fire was associated with the presence of shrub or not and then modelled a subset of the data where the height was greater than zero.

Second, we investigated the association between vegetation and butterfly diversity at the transect level, using the full dataset (*n* sites = 58). Our response variables were butterfly species richness and butterfly abundance per transect, and our explanatory variables were the vegetation variables (Table 1). We used generalized linear mixed models with a Poisson distribution for species richness and a negative binomial distribution for species abundance (Warton et al., 2016), treating fragment, survey round and grazing regime as random factors.

TABLE 1 Vegetation variables sampled in each plot in each renosterveld study site (40 plots per site in total)

Vegetation variable	Description
Number of plant species	We counted the number of different plant species present in the plot. We verified plant species counts by having two fieldworkers make separate counts of the same plot
Number of flowers	We pooled the number of flowers of all plant species in the plot. We considered one floral unit as a visible single head of a flower. Where species had multiple small flowers in clusters, for example *Hymenolepis spp*, we estimated the number of flowers in a single cluster and multiplied by the number of clusters. Where there were too many flowers to accurately and efficiently count (>500), we approximated by counting a smaller area of the plot and scaling up to the plot area (4 m^2)
Shrub height	We placed a 2-m ruler at five random locations in the plot and measured the shrub height. We determined shrub as vegetation having woody stems and usually identified as *Elytropappus rhinocerotis*, *Galenia africana*, *Eriocephalus africanus* or *Searsia* spp. We later summed and averaged these five measurements to get the mean shrub height for each plot
Non-shrub vegetation height	We did the same as above for all other vegetation in the plot, including graminoids and forbs
% vegetation cover	The estimated proportion of the sample plot covered by vegetation, the remainder being bare soil or rock.

Where species richness data were underdispersed, we used a generalized Poisson distribution (Harris et al., 2012). We observed very high abundances of Painted Lady (*Vanessa cardui)* in several sites due to migration, thus removed this species from our analyses to reduce anomaly (Öckinger & Smith, 2007). We classified butterfly species into high and low mobility using information taken from the literature on body and wing size (Mercenero et al., 2013; Woodhall, 2005) and expert consultation (Table S1) and then applied the same analyses for high and low-mobility butterfly species separately.

Third, we investigated the association between time since last fire and landscape context with butterfly diversity. Each site was treated as an individual observation, using the same subset of the data as in step 1, with time since last fire as a continuous variable (n sites = 21). Our response variables were pooled butterfly species richness and pooled species abundance data at the site level, and our explanatory variables were time since last fire and natural habitat in the surrounding landscape. We again included grazing as an explanatory variable rather than a random effect, although we did not design the study to test this variable. We chose to use the amount of natural habitat in the surrounding landscape as an explanatory variable because butterflies are a generally mobile taxon and many species are able to cross different habitat types. This variable was highly correlated with fragment size (0.89 Pearson's correlation coefficient); therefore, we did not include fragment size into the models. As before, we used generalized linear mixed models with a Poisson distribution for species richness and a negative binomial distribution for species abundance, treating fragment and grazing regime as random factors. We tested for interactions between time since fire and landscape context. We also tested for a unimodal relationship of time since last fire by including a quadratic term in the model equations. We then applied the same analyses for high and low-mobility species separately. In all models for steps 1–3, we checked for correlation between explanatory variables and where variables were considered to be correlated (>0.5 Pearson's correlation coefficient), we included only one variable in the model. We also made backwards stepwise selection to include only variables with statistically significant predictive power in our final models. We used the R package glmmTMB (Brooks et al., 2017).

In a fourth step, we analysed the six fragments which contained both a recently burned site (less than 6 years ago) and long-since burned site (more than 16 years ago). We tested differences in butterfly species richness and abundance between the paired sites with Student's t test. This enabled us to check the effect of fire on butterfly diversity without additional inter-fragment variability.

Lastly, to see whether species composition was associated with fire and landscape context, we performed non-multi-dimensional scaling (NMDS) analysis and fitted site-level environmental variables (i.e. time since last fire and natural habitat in the surrounding area, Supplementary Material 1) with a permutation test using the function *envfit* in the vegan package in R (Oksanen et al., 2019). We used a "Bray–Curtis" dissimilarity index to indicate dissimilarity among sites. In order to include all observed species in the ordination, we included all surveyed sites (n = 58) and for sites in which fire occurred more than 16 years ago, we considered them as 20 years since last fire. We performed all analyses in R Version 3.6.1 (R Core Team, 2020).

3 | RESULTS

We observed 6,131 butterfly individuals (excluding *Vanessa cardui*, 9,273 individuals) during the survey period from a total of 29 species and five families (for full species list see Supplementary

TABLE 2 Summary table of predicted effects of fire on renosterveld vegetation at transect level. Each row corresponds to one model

Response variable	Model performance		Model coefficients											
			(Intercept)				Time since last fire				Grazing lightly grazed				Grazing heavily grazed			
	R^2 cond.	R^2 marg.	Est	*SE*	*z*	*p*	Est	*SE*	*z*	*p*	Est	*SE*	*z*	*p*	Est	*SE*	*z*	*p*
No. plant species	0.49	0.05	2.43	0.12	20.63	**<0.001*****	−0.02	<0.01	−5.11	**<0.001*****				ns				ns
No. flowers	0.28	<0.01	4.31	0.32	13.27	**<0.001*****				ns				ns				ns
Presence of shrub	0.63	0.46	−0.63	0.41	−1.51	0.13	0.41	0.06	6.56	**<0.001*****				ns	−2.1	1.02	−2.06	0.04*
Shrub height	0.43	0.34	38.42	2.47	10.44(t)	**<0.001*****	2.83	0.27	10.44(t)	**<0.001*****				ns				ns
Non-shrub vegetation height	0.19	0.07	21.43	1.32	16.24	**<0.001*****	0.56	0.1	5.45	**<0.001*****				ns				ns
Vegetation cover (%)	0.47	0.3	0.38	0.03	12.6(t)	**<0.001*****	0.03	<0.01	12.22(t)	**<0.001*****				ns				ns

Note: Highly statistically significant *p*-values are shown in bold. Levels of significance are indicated by stars (.<0.1; *<0.05; **<0.01; ***<0.001). "na" = not available, "ns" = non-significant. Z values are shown except for linear models where the t-value is shown. Intercept for site-level models includes first level of grazing effect, that is non-grazed sites.

Material 2). Butterfly abundance was highest in the second survey round (2,598 individuals), from 27/09/18 to 17/10/18. The highest number of species observed at one site was 14, the lowest was two and the median was six. We did not observe any species classified as Endangered, Vulnerable, Near Threatened or Rare according to Red List criteria (SALCA, 2017). Thirteen species were considered to be of high mobility and 17 considered to be of low to medium mobility.

We found that time since the last fire was significantly associated with all sampled vegetation variables except for number of flowers (Table 2). While increased time since fire was negatively associated with our observed plant species diversity, we found a positive association of time since fire with the presence of shrub, shrub height, the height of non-shrub vegetation and the proportion of vegetation cover within the plot. We also found a negative association of grazed sites with presence of shrub (Table 2).

Vegetation variables had mixed relationships with butterfly species richness and abundance (Table 3). We found a positive association between plant species richness and butterfly species richness and abundance at the transect level, for both high- and low-mobility butterfly species. For low-mobility butterfly species richness, we found a negative association with the proportion of vegetation cover. The number of flowers was significantly positively associated with butterfly species abundance, and to a lesser extent with butterfly species richness. We found a significant positive association between the height of non-shrub vegetation and our observed butterfly abundance, and a negative association with increasing vegetation cover. At site level, the amount of natural habitat in the surrounding landscape was positively associated with species richness (Figure 3) and to a lesser extent, low-mobility butterfly species abundance (marginally statistically significant). We found no association with the number of neighbouring fragments within a 5 km radius of our study sites and no interactive association of fire and natural habitat in the surrounding landscape. We found a negative association between time since last fire and low-mobility butterfly species richness, whereas we found a positive association of time since last fire with high-mobility species richness (Figure 3). Time since last fire was also significantly negatively associated with total butterfly species abundance. We did not find a significant relationship for a quadratic term of time since last fire and, therefore, could not confirm a unimodal relationship of time since last fire and butterfly diversity. These patterns were observed for up to 16 years but could not be confirmed for sites of more than 16 years, where variability in butterfly diversity may be driven by unknown successional age or other unknown factors.

We found that butterfly species richness and abundance differed between pairs of recently burned and old sites in the same fragment (Figure 4). Across all pairs, butterfly species abundance was significantly lower in sites where fires occurred more than 16 years ago ($t = 2.62$, $p = 0.046$), whereas species richness did not differ significantly between paired sites ($t = 0.73$, $p = 0.49$). Median butterfly species richness was 5 in sites 0–6 years and 6 in sites of 16+ years. Median butterfly abundance was 106.5 in sites of 0–6 years and 98.5 in sites of 16+ years.

TABLE 3 Summary table of predicted effects of vegetation (transect level) and landscape (site level) predictor variables on butterfly species richness and abundance

	Model performance		Model coefficients							
			(Intercept)				No. of plant species			
Response variable	R^2 cond.	R^2 marg.	Est	*SE*	z	*p*	Est	*SE*	z	*p*
Transect										
Butterfly species richness (total)	0.29	0.03	−0.53	0.22	−2.34	0.02*	0.04	<0.01	5.73	**<0.001*****
High-mobility species richness	0.52	<0.01	−1.12	0.5	−2.25	0.02*	0.02	<0.01	2.81	<0.01**
Low-mobility species richness	0.37	0.03	−1.87	0.43	−4.35	**<0.001*****	0.06	0.01	4.96	**<0.001*****
Butterfly abundance (total)	0.5	0.06	−0.14	0.3	−0.46	0.64	0.05	<0.01	6.95	**<0.001*****
High-mobility species abundance	0.71	0.01	−0.71	0.65	−1.08	0.28	0.03	<0.01	3.93	**<0.001*****
Low-mobility species abundance	0.49	0.06	−1.94	0.52	−3.73	**<0.001*****	0.09	0.01	6.19	**<0.001*****
	Model performance		**Model coefficients**							
			(Intercept)				**Natural habitat (sqrt)**			
Response variable	R^2 **cond.**	R^2 **marg.**	**Est**	***SE***	**z**	***p***	**Est**	***SE***	**z**	***p***
Site										
Butterfly species richness (total)	na	0.44	1.65	0.18	9.31	**<0.001*****	0.02	<0.01	2.37	<0.02*
High-mobility species richness	0.79	0.53	0.41	0.16	2.52	**0.01***	0.02	<0.01	2.89	<0.01**
Low-mobility species richness	na	0.39	1.35	0.21	6.29	**<0.001*****	0.03	0.01	2.46	<0.05*
Butterfly abundance (total)	na	0.41	5.11	0.17	29.35	**<0.001*****				ns
High-mobility species abundance	na	0.17	4.66	0.19	23.42	**<0.001*****				ns
Low-mobility species abundance	0.96	0.53	3.18	0.39	8.18	**<0.001*****	0.04	0.02	1.74	0.08.

Note: Effects were generated from generalized linear mixed models selected following backwards stepwise selection, so final models included only statistically significant variables. Each row corresponds to one model with included predictor variables. Highly statistically significant *p*-values (***<0.001) are shown in bold. Levels of significance are indicated by stars (.<0.1; *<0.05; **<0.01; ***<0.001). "na" = not available; "ns" = non-significant. Intercept for site-level models includes first level of grazing effect, that is non-grazed sites.

The NMDS suggests that renosterveld butterfly composition is also associated with time since last fire and the amount of natural habitat in the surrounding landscape (Figure 5). There appears to be little clustering of species according to mobility, although high-mobility species including the Common meadow white (*Pontia helice*), the Painted Lady (*Vanessa cardui*) and the Boland Brown (*Melampias huebneri*) appear to be more associated with increased time since fire. Certain species appear to be associated with sites with more natural habitat in the surrounding landscape, such as the Boland Skolly (*Thestor protumnus*) and the Protea Emperor (*Charaxes pelias*). Other low-mobility species were scattered across even small or isolated sites without much natural habitat in the surrounding. The divergence of the fitted variables (time since last fire and surrounding natural habitat) suggests compositional dissimilarity among sites where fires occurred more than 16 years ago and sites with more natural habitat in the surrounding landscape; both fitted variables were significant at $p < 0.05$.

4 | DISCUSSION

Our results showed that fire plays a role for vegetation and butterfly diversity in renosterveld fragments at both the local and landscape level. Fire was consistently associated with vegetation

No. of flowers				Non-shrub vegetation height				Vegetation Cover			
Est	*SE*	z	*p*	Est	*SE*	z	*p*	Est	*SE*	z	*p*
<0.01	<0.01	1.86	0.06.				ns	<−0.01	<0.01	−2.58	<0.01**
			ns				ns				ns
			ns				ns	<−0.01	<0.01	−4.86	**<0.001*** **
<0.01	<0.01	4.83	**<0.001*** **	<0.01	<0.01	3.87	**<0.001*** **	<−0.01	<0.01	−2.09	<0.05*
<0.01	<0.01	3.89	**<0.001*** **	<0.01	<0.01	2.91	0.02**				ns
			ns	0.01	<0.01	2.72	0.01**	−0.01	<0.01	−6.28	**<0.001*** **

Time since last fire				Grazing Lightly grazed				Grazing Heavily grazed			
Est	*SE*	z	*p*	Est	*SE*	z	*p*	Est	*SE*	z	*p*
			ns				ns	−0.71	0.43	−1.66	0.09.
0.03	0.01	2.13	0.03*	0.41	0.22	1.85	0.06.				ns
−0.06	0.02	−2.25	0.02*				ns				ns
−0.06	0.02	−2.57	0.01*				ns	−0.64	0.37	−1.73	0.08.
−0.05	0.03	−1.71	0.09.				ns				ns
−0.08	0.01	−5.3	**<0.001*** **				ns	−1.46	0.69	2.1	0.04*

change in our study, which demonstrates the transformative effect of fire in the renosterveld ecosystem (Cousins et al., 2017; Curtis et al., 2013; Kraaij & van Wilgen, 2014). We hypothesized that fire would be positively related to renosterveld plant diversity, which in turn may be associated with higher butterfly diversity through the emergence of attractive floral resources and larval food plants. Indeed, the associations we observed between vegetation and butterfly species richness and abundance demonstrate how fire may be indirectly related to renosterveld butterfly diversity through vegetation. At the transect level, plant diversity was positively associated with both butterfly species richness and abundance, while flower abundance was important for butterfly abundance, although it was not associated with fire. Fire adaptation among renosterveld plant species is complex, due to the exceptional endemism and wide range of reproductive traits including re-seeding and sprouting, which may be fire-adapted through responses to heat and smoke (Cousins et al., 2017). For example, *Protea* spp. are present in many renosterveld-fynbos transitional areas, are fire-adapted and are also host plants for endemic CFR butterflies such as the orange-banded protea (*Capys alpheus alpheus*) (Mercenero et al., 2013).

The change in vegetation structure and increase in openness immediately following a fire may indirectly benefit butterflies also by providing opportunities for activities such as patrolling and

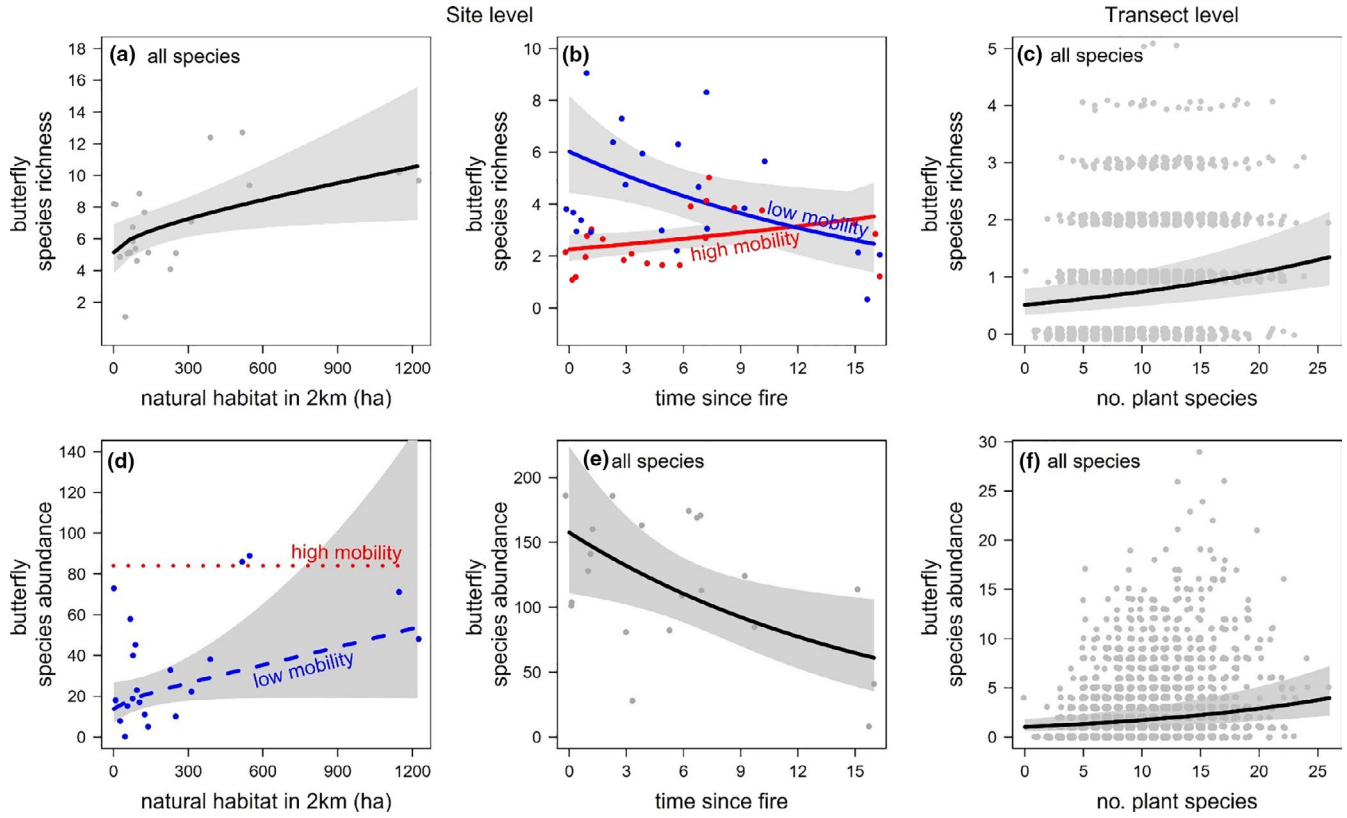

FIGURE 3 Predicted effects from the fitted generalized linear models for the amount of natural habitat in the surrounding landscape; the time since last fire and the number of plant species on butterfly richness (top row) and abundance (bottom row). Only relationships that were statistically significant are shown. Points show individual observations. Grey bands show 95% confidence intervals. Site-level model graphs (panels A, B, D and E) show total butterfly species richness and abundance per site; transect level model graphs (panels C and F) show butterfly species richness and abundance per transect. Black lines refer to total butterfly species; red lines refer to high-mobility butterfly species and blue lines refer to low-mobility butterfly species. Red dotted line (panel D) shows mean high-mobility species abundance across all sites for comparison with modelled low-mobility species abundance (blue dashed lines, $p < 0.1$)

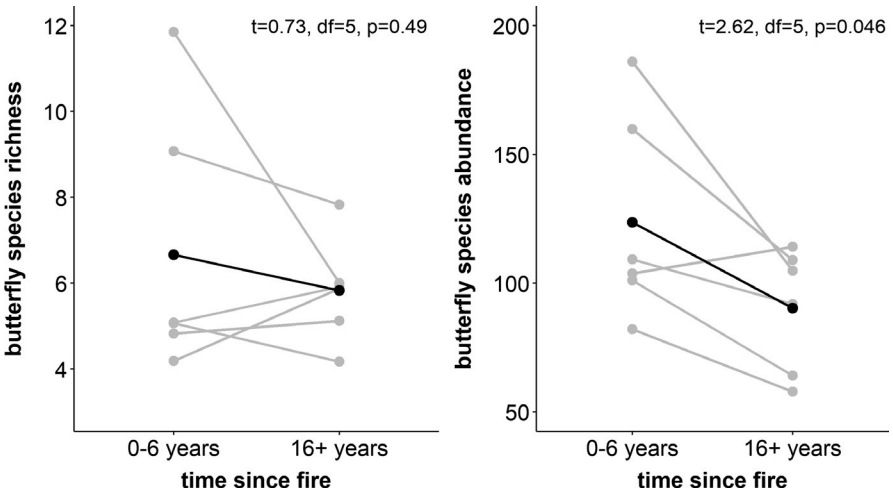

FIGURE 4 Difference in total butterfly species richness (left) and abundance (right) between pairs of sites in the same fragment ($n = 6$). Sites were burned either 0–6 years ago or more than 16 years ago. The difference for abundance between pairs of sites was significant in a paired *t* test ($p < 0.05$). Means are shown as black circles and linked with black lines. Original data points are shown as grey points. Grey lines link data points from pairs of sites and indicate general direction of trend

basking (Dennis, 2004; Gillespie & Wratten, 2012). We found that time since fire was significantly negatively associated with vegetation cover, which in turn was negatively associated with butterfly species richness and abundance. Low-mobility species were particularly negatively associated with increased vegetation cover. This trend could be due to the lack of gaps for host plants, upon which the abundance of low-mobility species and habitat specialists is particularly dependent (Curtis et al., 2015). The removal of shrub and other vegetation through fire creates gaps in renosterveld for the establishment of annuals, including *Poaceae* grasses (Cousins et al., 2017) and *Crassulaceae* spp. (Krug, 2004), which are larval host plants for observed butterfly species including

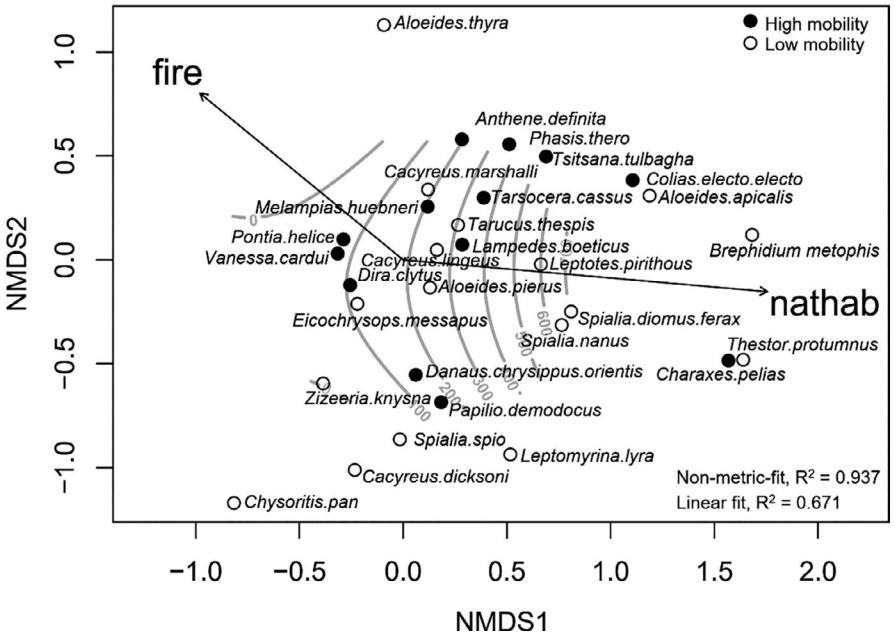

FIGURE 5 Non-metric multidimensional scaling of butterfly species with fitted environmental variables (significant at < 0.05), "fire" = time since the last fire in years, "nathab" = amount of natural habitat in the surrounding 2km from the survey location. Contours of modelled natural habitat amount (hectares) are shown in grey, increasing from left to right (0–600 ha) in the ordination

the Tulbagh Sylph (*Tsitana tulbagha tulbagha*) and Cape Black-eye (*Leptomyrina lara*). However, structural heterogeneity in renosterveld fragments may also be beneficial for butterflies, as shrub components including *Elytropappus rhinoceritis* may act as nurse plants for other renosterveld plant species (Simons, 2017). Mature shrubs can also provide high numbers of pollinator-attracting flowers, which may explain why we found no association between fire and flower abundance.

In addition to these indirect associations between fire and butterflies via vegetation, fire may directly affect butterfly populations by loss of individuals at egg and larval stages. Adult butterflies (imago), as mobile taxa, may be able to escape fire and to quickly recolonize, unlike many other pollinators which may be limited in their dispersal ability (Johansson et al., 2020; Steffan-Dewenter et al., 2002). Greater proximity and amount of neighbouring habitat can allow for recolonization of recently burned patches by butterfly species (Moranz et al., 2014). We hypothesized that natural habitat would be positively associated with butterfly diversity in focal fragments. Our study found that natural habitat in the surrounding landscape was positively associated with overall butterfly species richness. We also observed that overall butterfly abundance is negatively associated with time since last fire, and that in large fragments where one part has been burned, butterfly abundance is higher than in the remaining area which remains late-successional. These observations suggest the importance of the availability of good quality habitat within large habitat fragments and also in the landscape for butterfly populations (Kormann et al., 2019; Pocewicz et al., 2009), particularly for highly fragmented Mediterranean-type ecosystems where surrounding land use may be intensive (e.g. Fernández-Chacon et al., 2014; Stefanescu et al., 2004). Renosterveld fragments in the surrounding landscape to the focal fragment are a potential pollinator source for renosterveld plant species, suggesting that landscape context plays an important role for mutualistic species relationships (Donaldson et al., 2002). Therefore, while vegetation structure at the local scale is crucial in providing suitable habitat quality, which affects butterfly diversity, this cannot be considered in isolation to landscape-level attributes (Loos et al., 2014; Öckinger & Smith, 2007; Steffan-Dewenter et al., 2002), particularly when the landscape is fire-prone and successional stage can alter habitat quality.

We also hypothesized disturbance through fire to be more strongly negatively associated with low-mobility species than high-mobility species. We found that high-mobility (as proxy for larger body and wing size and stronger fliers) species richness was positively associated with time since last fire. The highly mobile species observed in our study sites included the Common Meadow White (*Pontia helice*) and the Citrus Swallowtail (*Papilio demodocus*), the larvae of which feed on Brassicaceae and cultivated *Citrus* spp, respectively, and may therefore persist in agricultural landscapes without the need to use renosterveld. As suggested by the results of our NMDS, highly mobile species such as *Melampias huebneri* and the Spring Widow (*Tarsocera cassus*) are able to roam in search for habitat and therefore may be present in late-successional fragments or more isolated fragments. We found that low-mobility (as proxy for decreasing body size and migrational ability) butterfly species were positively associated with increasing natural habitat in the surroundings and, similar to Steffan-Dewenter and Tscharntke (1997), were negatively associated with increasing successional age. However, low-mobility species varied from generalist and widespread species to colonial species with limited ranges. Thus, although body and wing size may differ among species, other traits leading to successful dispersal may drive functional butterfly diversity in remaining renosterveld. For example, small weak fliers such as the Cupreous Blue (*Eiochrysops messapus*) and the Fynbos Blue (*Tarucus thespis*) rely on larval host plant species from the genera *Thesium* and *Phylica*, respectively, both of which widely occur in Western Cape fynbos and renosterveld (Mercenero et al., 2013), and are fire-adapted.

Thesium species are able to reappear following fire due to long-lived seedbanks, and *Phylica* species may be obligate reseeders or ant-dispersed (Kraaij & van Wilgen, 2014). Daily foraging patterns of generalist butterflies with widespread larval host plants, such as the African Grass Blue (*Zizeeria knysna*), which also occur in disturbed agricultural lands, may also support dispersal. Additionally, many low-mobility butterfly species we found, such as *Thestor protumnus* and *Aloeides* spp., have obligative or associative associations with ant colonies (Edge & van Hamburg, 2010). Ants may be particularly resilient to fire in the CFR (Pryke & Samways, 2012). Successful ant colony survival or colonization following disturbance through fire may thereby support the favourable conditions for these butterflies' colonization of remaining fragments.

4.1 | Implications for management

Resilient agricultural landscapes that support biodiversity would ideally consist of a mosaic of well-connected early- and late-successional habitats, ensuring that recolonization can take place following disturbance (Bengtsson et al., 2003; Tscharntke et al., 2005). However, fire can be viewed as problematic in fragmented agricultural landscapes, where it can pose a threat to crops, livestock and humans (van Wilgen et al., 2010). Current renosterveld conservation management, which includes prescribed burning, is mostly focused on the large remaining fragments. Small fragments are nonetheless important for collective butterfly diversity across the target landscape (Fahrig, 2020; Topp & Loos, 2019b), and it is therefore key to ensure a range of successional ages and structural heterogeneity across all fragment sizes, as part of landscape-scale conservation strategies (e.g. von Hase et al., 2003). Some Swartland renosterveld fragments may be designated as nature or biosphere reserves, although this term covers a broad range of management activities of which prescribed burns are not necessarily an integral part. Renosterveld is considered to be of little use by many land managers and largely left unattended, which may be in part due to lack of clarity on the necessity to burn and the associated risks (Cousins et al., 2017; van Wilgen, 2013).

Farmers in the Swartland annually burn their wheat fields following harvest, a practice which some consider outdated and harmful to soils, but may provide an opportunity for controlled burns to take place in renosterveld patches adjacent to farmland. Conservation practitioners recommend to burn renosterveld every 10–15 years to regenerate plant diversity (Curtis, 2013; Esler et al., 2014; Kraaij & van Wilgen, 2014), which our results suggest would also benefit butterflies. Our results suggest that more frequent burns may be particularly positively associated with butterfly abundance, while the range of responses of butterfly richness suggest that some sites older than 16 years may also host diverse butterfly populations. For example, burning areas within fragments every 10 years or so could support low-mobility butterfly species, while high-mobility species may persist in fragments with burns of 15 years or more. Such a mosaic approach to fire regime would increase the diversity of renosterveld structures and may cater for different habitat preferences of various butterfly species, while corresponding to recommendations for plant diversity.

Ideally, butterfly surveys would take place before prescribed burns, in order to assess potential impacts. For example, while widespread species may be able to recolonize following a burn, rare or highly specialized species may struggle to recolonize if there is a lack of metapopulations, such as the case of the Brenton Blue butterfly (*Orachysops niobe*) elsewhere in South Africa (Brenton Blue Trust, 2019). Some lycaenid species that we observed, such as *Thestor protumnus* and *Chysoritis pan*, have strictly colonial population structures of limited area and may be particularly vulnerable to direct mortality due to fire. In this case, it may be beneficial to burn partially without disturbing the colony, but still providing habitat heterogeneity, as recommended for single species conservation elsewhere (e.g. New et al., 2010). Our study investigated the time since previous burn of all sites. We did not investigate the relationships of butterfly diversity to repeated short-term burns in renosterveld, which would be an important step for future research. Moreover, ecologically appropriate fire regimes must be complemented by supportive grazing regimes so that regeneration of plant diversity is not mitigated by livestock grazing too soon following a burn (Curtis, 2013; Esler et al., 2014).

Our data reflect the heterogeneous nature of the agricultural landscape in question; however, to further study the effects of grazing and its interaction with fire on renosterveld vegetation, butterflies and other associated insects, an experimental design of treatment plots including burning and grazing treatments and control plots could be used in further research. This could also address some of the study limitations given that our study design was observational rather than experimental in nature. Similar to previous studies of fire ecology and invertebrates (e.g. Adedoja et al., 2019), the interpretation of our findings may be limited given the potential influence of other environmental factors. For example, the sites of different fire ages were not randomly distributed throughout the landscape and surrounding land use, soil types and microclimate were not controlled for. It is important to note that our findings indicate associations rather than causal relationships.

In summary, landscape context and fire regime are associated with butterfly species richness and abundance in renosterveld fragments, both directly and through changes to vegetation. Conservation activity including prescribed burns, which aim to regenerate plant diversity, may therefore benefit butterfly diversity. Butterflies should be considered within the scope of fire management for fire-adapted renosterveld plant diversity. For example, butterfly surveys for rare, habitat specialists or small colonies could be conducted before burning large patches of renosterveld for plant regeneration. In this intensively farmed landscape, remaining large and small renosterveld fragments must be sensitively managed with fire and livestock in order to support landscape-wide biodiversity.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY

Data available on request from the authors.

ORCID

Jacqueline Loos https://orcid.org/0000-0002-7639-2894

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BIOSKETCH

Emmeline N. Topp is a researcher with interests in biodiversity conservation in agricultural landscapes and the relationships between people and nature. Teja Tscharntke is a professor of Agroecology with a research focus on local and landscape management for biodiversity, pollination, biocontrol and social–ecological trade-offs in human-dominated landscapes. Jacqueline Loos is a landscape ecologist and investigates relationships between the biophysical environment and human land use within dynamic social–ecological systems.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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